Vol. 40 No. 3

BULLETIN

OF THE

TORREY BOTANICAL CLUB

MARCH 1913

Development of the peristome in Ceratodon purpureus

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INTRODUCTORY

In his recent work on the Bryophyta, Cavers ('11, p. 182) divides the Bryales, or true mosses, into the four following groups, based on distinctions emphasized by Fleischer: Tetraphidales, Polytrichales, Buxbaumiales, and Eu-Bryales. In this division the peristome is the organ from which the most important differential characters are derived. In the Tetraphidales and Polytrichales the teeth of the peristome are composed of entire cells; in the Buxbaumiales and Eu-Bryales they are composed of thickened cell walls. Leaving the Encalyptaceae out of consideration, the Eu-Bryales may be further divided, following the example of Philibert ('84, p. 67), into the Diplolepideae and the Haplolepideae. The Diplolepideae with few exceptions have two peristomes, while the Haplolepideae have single peristomes, if such structures are present at all.

In the Diplolepideae the two peristomes are derived from two concentric layers of cells in the opercular portion of the capsule. The development of the peristome has been described in several species of this group but is especially well known in *Funaria hygrometrica* (Goebel, '87, p. 188; Campbell, '05, p. 211) and *Mnium hornum* (Strasburger, '02, p. 491), which may be considered typical representatives. In both these species the outer peristomial layer is composed of thirty-two longitudinal rows of cells and the inner of sixteen rows. These rows form sixteen groups,

[The BULLETIN for February 1913 (**40**: 43–96) was issued March 18.]

each of which in cross section shows two cells of the outer layer lying opposite one cell of the inner layer. One of the sixteen teeth of the outer peristome arises in each group and is formed by the deposition of longitudinal bands of thickening upon the periclinal walls between the peristomial layers. These bands taper to fine points from a broader base. The band deposited by the two outer rows is of fairly uniform thickness throughout and extends as a continuous layer across the thin radial and transverse walls separating the cells. The band deposited by the single inner row corresponds in position and in width with the one just described and is of about the same thickness. Thickening is deposited also upon the transverse walls separating the cells of this row. Upon the disappearance of the portions of the walls which have remained thin the teeth show their mature condition. Each tooth bears upon its inner surface a series of transverse ridges corresponding to the thickened transverse walls, while the smooth outer surface shows the vestiges of the transverse and radial walls, the latter appearing as a zigzag median line running the entire length of the tooth. The delicate inner peristome is formed by deposits of thickening upon the inner walls of the inner peristomial layer. Toward the base the thickening is continuous, but in the upper part it is in the form of isolated longitudinal bands, definite in position and in number. At maturity the continuous portion forms the basilar membrane of the peristome, while the isolated bands form the segments and the cilia.

In the Haplolepideae the peristome is likewise derived from two concentric layers of cells, but in this case each tooth is formed by one row of outer cells and two rows of inner cells and therefore shows the zigzag longitudinal line on the inner surface instead of on the outer. In the opinion of Philibert ('88, p. 68), the single peristome of this group is homologous with the inner peristome of the Diplolepideae. This being the case it is evident that the large-celled inner peristomial layer in the Diplolepideae would be homologous with the large-celled outer layer in the Haplolepideae. The subject of the present study, *Ceratodon purpureus*, is a characteristic member of the Haplolepideae, and many of the features which the peristome shows, in development as well as in structure, are undoubtedly common to other species of the group.

The material, which was collected in the vicinity of New Haven, Connecticut, was studied by means of microtome sections.

The mature peristome of *Ceratodon purpureus* has been repeatedly described in taxonomic treatises, but a brief account of its peculiarities will make the description of the development more intelligible. It consists of sixteen teeth which arise from a continuous basilar membrane. Each tooth is divided almost to the base into two slender tapering branches, which show much the same structure throughout their entire length (FIG. 17, 18). The outer portion of each branch forms a subcylindrical ridge, distinctly contracted at its union with the inner portion, which is broader and more flattened toward the base. Four or five corresponding transverse ridges extend across the branches of each tooth, being close together at the base but farther apart toward the apex. They correspond with the transverse walls of the outer peristomial layer. On the inner surface also vestiges of transverse walls can be detected, but these are unaccompanied by ridges (FIG. 19, 24). Just above the basal undivided portion of each tooth one or more of the transverse ridges extend across from branch to branch, thus leaving median perforations (FIG. 21). The basal portion is especially thick and bears several crowded transverse ridges, which in longitudinal section give the tooth a serrated appearance (FIG. 24). The entire surface of the teeth is covered over with minute spicules. The basilar membrane of the peristome is in the form of a hollow cylinder, sixteen cells in circumference and three or four cells high, representing a part of the outer peristomial layer. The thickened walls in this portion of the peristome are smooth throughout.

The early development of the sporophyte in *Ceratodon purpureus* was studied by Kienitz-Gerloff ('78, p. 42), who detected in very young stages a two-sided apical cell cutting off two rows of segments, just as in other members of the Eu-Bryales. Each of these segments, as he further showed, soon became divided into quadrants by an anticlinal wall and then underwent divisions according to the so-called "Grundquadrat" or "fundamental square" method described below. The embryonic development of *Ceratodon* is discussed also by Goebel ('87, p. 178), but the most complete account of the process is that published by Kuntzen ('12), who, however, pays but little attention to the peristome.

The first developmental study of the peristome in *Ceratodon purpureus* was made by Lantzius-Beninga ('50, p. 574), who compared it with the peristome of *Trichostomum tortile*, now known as *Ditrichum tortile*. In his figures of young transverse sections ('50, *pl. 66, f. 40, 41*) he indicated the two layers of cells which give rise to the peristome but represented each layer as being composed of sixteen cells, those of the inner layer alternating with those of the outer. This was proved to be incorrect by Kienitz-Gerloff ('78, p. 44), who stated that, while the outer layer showed sixteen cells in section, the inner showed from twenty to twenty-four cells and that normally two cells of the outer layer bounded three cells of the inner. He showed further that the peristome developed in the amphithecial portion of the sporophyte and that the peristomial cells represented the fourth and fifth layers from the outside except in the region of the operculum, where they represented the third and fourth layers. The studies of Lantzius-Beninga and Kienitz-Gerloff have to do mainly with the region where the peristome is formed and give but few details about the actual development of the teeth, and the same thing is true of most of the work which has been done upon the peristomes of other Haplolepideae.

In the present paper the account of the peristome will be divided into two parts. In the first the origin and development of the two peristomial layers will be described; in the second the deposition of the thickenings which constitute the bulk of the teeth will be considered.

DEVELOPMENT OF THE PERISTOMIAL LAYERS

As earlier writers have pointed out, the divisions which take place in the segments cut off from the apical cell of the young sporophyte proceed with great regularity, whether the segment is destined to form a part of the stalk or of one of the regions of the capsule. This regularity is characteristic not only of an individual species of the Bryales but of the group taken as a whole. It has been recently emphasized by Kuntzen ('12) in the particular case of *Ceratodon purpureus* and becomes strikingly evident through the study of the operculum and peristome. The opercular segments, like those which go to form the spore-case, are in

the form of half-cylinders, which become divided into quadrants by anticlinal walls. Cross sections through young sporophytes just below the apical cell show this condition clearly (FIG. 1, 2). It is in the quadrants that the division takes place according to the "fundamental square" method. If transverse walls are left out of consideration each quadrant divides by an anticlinal wall, extending as a curved surface from one of the side walls to the outside wall, into two cells (FIG. 3), a smaller triangular cell (as seen in section) and a larger four-sided cell. The latter soon divides by a periclinal wall into an outer and an inner cell (FIG. 4). According to Kuntzen ('12, p. 19) the segments in the stalk sometimes divide in the way just described and sometimes by means of a periclinal wall followed by an anticlinal wall in the outer of the two cells thus formed. In the spore-case he finds the second method only but admits that perhaps the first method is sometimes followed. In either case, after the rearrangement of the walls, the cross section shows four inner cells, the "fundamental square," surrounded by eight outer cells. The inner cells constitute the endothecium and the outer cells the amphithecium. A similar arrangement of the cells can be demonstrated in the young sporophytes of most of the higher bryophytes.

In the next stage of development the amphithecial cells divide by periclinal walls, thus giving rise to two layers of eight cells each (FIG. 5). The inner cells, shaded in the figure, will develop into the inner peristomial layer. The corresponding layer in the spore-case gives rise to the outer spore-sac. It is upon the periclinal walls separating the two amphithecial layers that the teeth of the future peristome will be deposited. Marked differences occur in the endothecium and amphithecium with respect to the relative rate of cell division. In the region of the annulus the inner peristomial layer completes its divisions before the endothecium has passed beyond the four-celled stage. In the region of the peristomial teeth the division may be simultaneous or the endothecium may divide first. In the portion of the operculum above the peristome the inner amphithecial layer never passes beyond the eight-celled stage.

In the region of the teeth, after the stage shown in FIG. 5, the cells of the outer amphithecial layer divide by anticlinal walls,

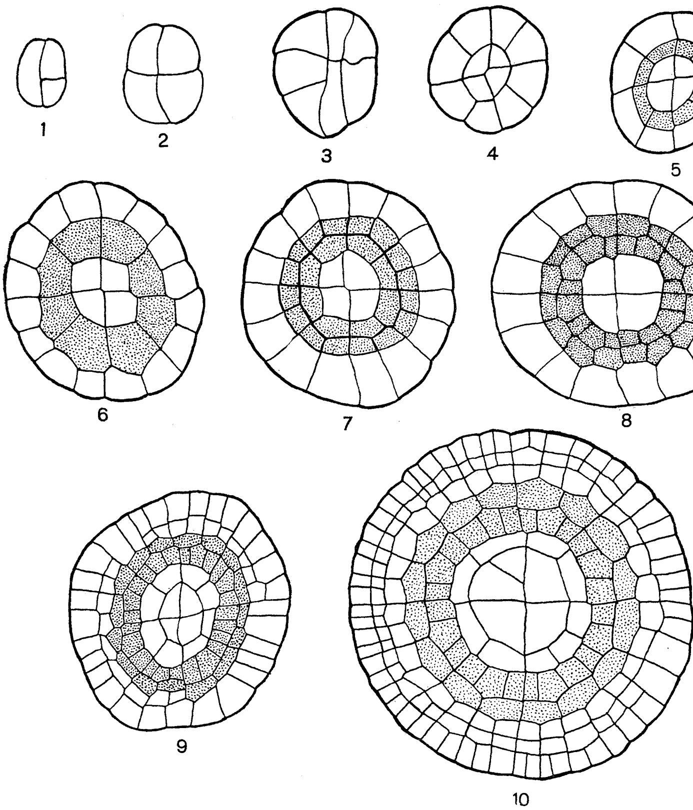

FIG. 1–10. Cross sections through the opercular region of young capsules, showing successive stages of development; peristomial layers stippled, ×300. 1 and 2, division of segments into quadrants; 3 and 4, establishment of amphithecium and endothecium; 5, establishment of inner peristomial layer; 6, division of cells in outer amphithecial layer by anticlinal walls; 7, establishment of outer peristomial layer; 8 and 9, division of cells in inner peristomial layer by anticlinal walls; 10, continuation of divisions in outer amphithecial layer and in endothecium.

thus raising the number of cells in this layer to sixteen (FIG. 6). Each of the sixteen cells then divides by a periclinal wall so that two layers of sixteen cells each are formed (FIG. 7). The inner layer represents the outer peristomial layer and undergoes no further divisions. It will be noted that the eight pairs of cells in this layer lie opposite the eight cells of the inner peristomial layer. In the spore-case the layer homologous with the outer peristomial layer gives rise to most of the photosynthetic tissue

including the large intercellular space. The condition shown in FIG. 7 corresponds closely with figures by Kienitz-Gerloff ('78, *pl. 1, f. 25b*) and Kuntzen ('12, *f. 10*), representing sections through the spore-case. The eight cells of the inner peristomial layer now proceed to divide in a very peculiar way. In each of these cells an anticlinal wall appears (FIG. 8), cutting off either to the right or left a small cell from one fourth to one third as wide as the parent cell. This is followed by a second anticlinal wall cutting off a similar small cell on the other side of the parent cell (FIG. 9). In this way the inner layer becomes divided into twenty-four cells, each group of three corresponding with one of the pairs of cells in the outer layer. No further divisions are undergone by these twenty-four cells. The arrangement of cells just described seems to be even more constant than Kienitz-Gerloff implies, since he states that the number of cells in the inner layer may vary from twenty to twenty-four.

The endothecium and the peripheral layer of the amphithecium play no direct part in the development of the peristome, and yet an account of the cell divisions that take place in them will not be wholly out of place. The divisions in the peripheral layer are not altogether definite. After the sixteen-celled stage, still shown in FIG. 8, the cells divide by anticlinal and periclinal walls without following a rigid system, adjacent cells often dividing in different ways (FIG. 10). In all cases, however, the final condition is essentially the same, three concentric layers of cells being produced. The outermost layer is composed of (approximately) 128 cells, the middle layer of 64 cells, and the innermost of 32 cells. In the region of the annulus, however, only two layers of cells are formed, thus allowing for the extraordinary development of the annular cells (FIG. 13, 25, 26). The peripheral layers of cells form the operculum, the external walls of the outermost layer becoming strongly thickened.

The divisions in the endothecium of the opercular region are essentially like those in the spore-case, as described and figured by Kuntzen ('12). After the four-celled stage, shown in FIG. 8, division takes place according to the "fundamental square" method, eight outer cells and four inner cells being thus formed (FIG. 9). The inner cells repeat this method of division (FIG. 10),

while the cells of the outer layer divide by anticlinal walls in a more or less indefinite manner. When the capsule approaches maturity the endothecial tissue within the peristome consists of a relatively small number of large and thin-walled cells, this tissue of course being the continuation of the columella and the sporogenous tissue in the spore-case.

While the segments have been undergoing the anticlinal and periclinal divisions just described, divisions by transverse walls have also occurred in the various layers. Apparently they occur in a rather indefinite way and vary in different parts of the capsule (see Kuntzen, '12, p. 22, etc.). In the peristomial layers transverse walls are especially numerous toward the base and tend, in this region at least, to be more numerous in the outer layer than in the inner (FIG. 13). Toward the apex they are more numerous in the inner layer (FIG. 12).

DEPOSITION OF THE PERISTOMIAL THICKENINGS

The forty rows of cells taking part in the formation of the peristome may be naturally divided into eight groups of five rows each. In each group three rows of the inner peristomial layer correspond with two rows of the outer layer. A cross section of such a group before the deposition of thickening is shown in FIG. 11. A group gives rise to two teeth of the peristome and the same processes are repeated in each group. The peristomial cells, before the thickenings are laid down, contain dense cytoplasm and small nuclei with several nucleoli but are usually without vacuoles (FIG. 11–13). In the upper part of the peristome, where the teeth are divided into branches, eight regions of thickening can be distinguished in each group, the four of the outer layer corresponding with the four of the inner layer. Two regions belong to each cell of the outer layer and to the median cell of the inner layer, while one region belongs to each lateral cell of the inner layer. The thickening first makes its appearance in the inner layer (FIG. 14) but soon becomes evident in the outer layer as well (FIG. 15, 16). If two corresponding regions are regarded as forming a single strand, each group will then form four strands, representing the four branches of the two peristomial teeth.

The deposition of thickening begins in the basal portion of

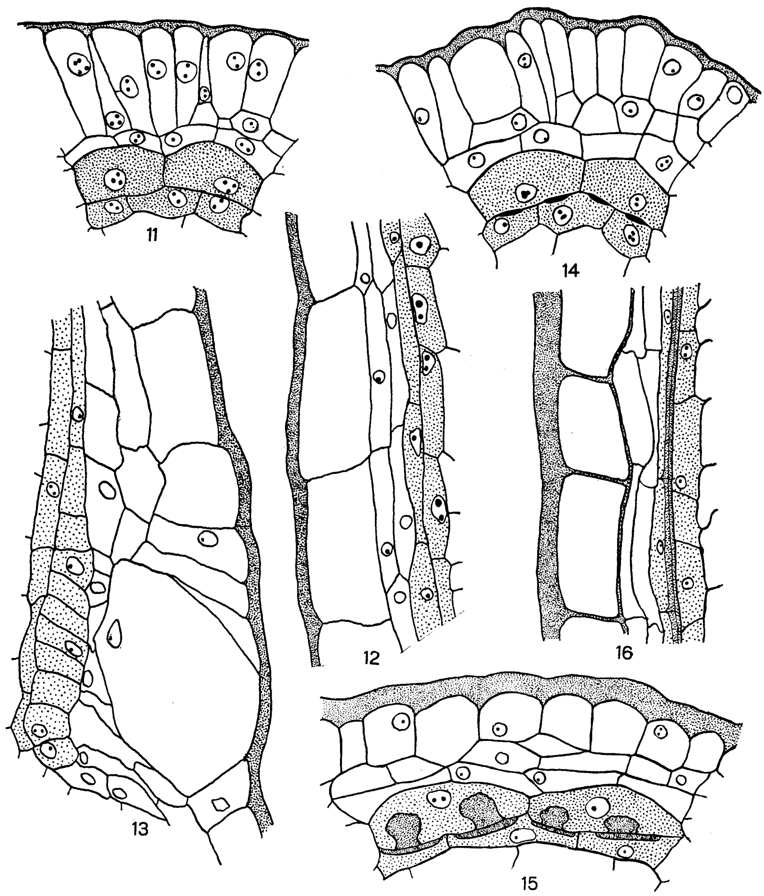

FIG. 11–16. Cross and radial sections through the amphithecial tissues of older capsules, ×300. 11 and 12, showing the peristomial layers in the region of the teeth, just before the deposition of the thickenings; 13, showing the same stage in the annular region; 14–16, showing early stages in the development of the thickenings.

the peristome but follows essentially the same method throughout the branches of the teeth. The portions of the strands deposited by the inner peristomial cells are broader than those deposited by the outer cells. They are therefore more conspicuous at first, but become less so later on. This is due to the fact that the inner portions of the strands develop to a slighter extent and in thickness only, while the outer portions give rise to the thick

subcylindrical ridges already noted in the mature teeth (FIG. 17). The differences between the inner and outer portions become less and less marked toward the apices of the branches (FIG. 18). Upon the transverse walls in the outer peristomial layer thickenings are also deposited. These are continuous with the thickenings on the inner wall and give rise to the transverse ridges of the mature teeth (FIG. 19). In a young stage, seen in tangential section (FIG. 20), the transverse thickenings apparently broaden out the outer longitudinal ridges, and the same appearance is even more

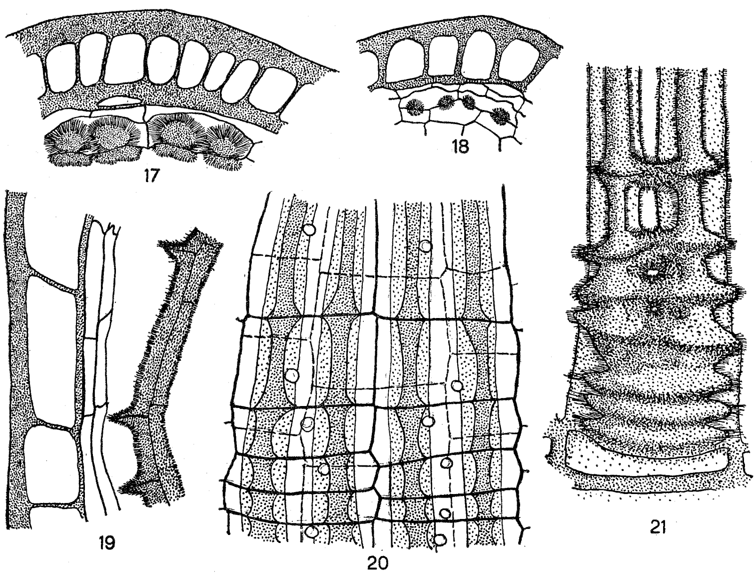

FIG. 17–19. Cross and radial sections in the region of the teeth, showing the peristomial thickenings in their final stage of development, ×300; 20, tangential view of young peristome, seen from the outside, ×300; 21, basal portion of a fully developed tooth, seen from the outside, ×300.

striking in an older tooth (FIG. 21). Toward the base of the branches the transverse ridges grow wider and wider until finally some of them span the distance between the branches and coalesce, thus forming a continuous ridge across the entire tooth. Below this region the ridges are all continuous. If Philibert's ideas regarding the homologies of the peristomial layers are accepted, it becomes evident that the transverse ridges just described correspond with those present on the inner surface of the outer peristome in the Diplolepideae. In *Ceratodon purpureus*, however, the

ridges become adherent to the inner walls of the peristomial layer instead of to the outer walls, as is the case in the Diplolepideae. In the lower part of a tooth the longitudinal ridges on the outside also show an increase in thickness until they extend more than half way across the cavities of the cells in which they are deposited (FIG. 22, on left). In the basal undivided portion of a tooth these ridges finally coalesce and form a single broad ridge (FIG. 22,

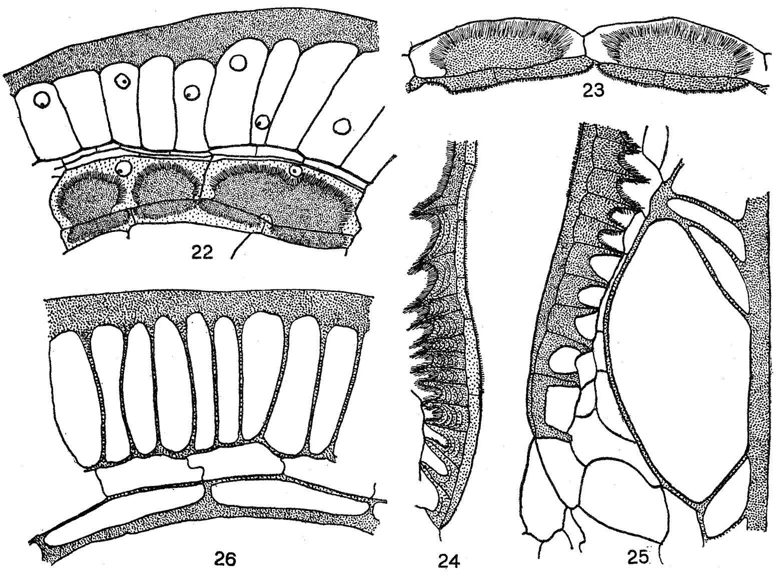

FIG. 22–26. Cross and radial sections in the region of the basal portion of the peristome, ×300. 22 and 23, showing the basal portions of two teeth; 24 and 25, showing the same, together with the basilar membrane; 26, showing the basilar membrane only.

on right, 23), beyond which the transverse ridges project for only a short distance (FIG. 24, 25).

The thinner deposits of thickening formed by the inner peristomial cells gradually increase in width toward the base until they finally meet and coalesce at the radial walls between the two rows of cells (FIG. 17, 22, 23). The vestiges of the radial walls form a zigzag longitudinal line on the inner surface of the tooth, and not on the outside as in the Diplolepideae. This line is of course much shorter than in *Funaria hygrometrica* and *Mnium hornum*, in which the teeth are not divided into branches. No

transverse ridges are developed in the inner peristomial layer, but the vestiges of the walls remain visible as fine lines.

When the strands of thickening have reached their full size, the spicules of cell wall substance are deposited in immense number over the entire surface (FIG. 17–19, 21–25). Those formed by the outer cells are considerably longer than those formed by the inner cells, but all are exceedingly minute.

The cells which form the basilar membrane of the peristome acquire thick walls also, but the deposits of thickening differ from those which form the teeth. This is especially true of the outer peristomial layer where the thickening extends almost evenly over the inner walls, the radial walls, and the transverse walls but leaves large pits on the outer walls (FIG. 25, 26). In the inner peristomial layer the thickening is less pronounced and forms a continuous layer over the outer wall. Throughout this portion of the peristome the surface of the thickening remains smooth, no spicules being developed. The basilar membrane lies just within the large cells of the annulus (FIG. 25).

Soon after the spicules have been deposited upon the teeth the peristomial cells dry up, the thin parts of the walls shrivel away and disappear, and the teeth become free. In the basilar membrane the pits in the outer wall now appear as perforations. At the same time the operculum becomes separated, and the endothecial tissues disintegrate. The finer structure of the mature peristome and the hygroscopic movements which it executes are fully described by Steinbrinck ('97).

SUMMARY

The original amphithecium, showing eight cells in cross section, divides by periclinal walls into an inner and an outer layer.

The inner peristomial layer develops from the inner amphithecial layer, undergoing division by anticlinal walls until it is composed of twenty-four longitudinal rows of cells.

The outer peristomial layer develops from sixteen longitudinal rows of cells cut off by periclinal walls from the outer amphithecial layer, after its eight rows have been divided by anticlinal walls; the outer peristomial layer undergoes no further divisions by anticlinal walls.

Ridges of thickening, representing the future teeth, are laid down upon the periclinal walls between the two peristomial layers.

The cells of the peristomial layers form eight groups, each composed of two rows of cells of the outer layer and three rows of the inner layer. Each group gives rise to two teeth.

In the upper part of each group eight deposits of thickening are laid down in four strands, representing the four branches of the two teeth; in the lower part only two strands are formed, representing the basal undivided portions of the teeth.

In the outer peristomial layer thickenings are deposited also upon the transverse walls, representing the transverse ridges of the teeth.

In the undivided basal portion of each tooth a fine median longitudinal line on the inner surface represents the vestiges of the radial walls between two rows of peristomial cells.

In the basilar membrane the thickening of the walls in the outer peristomial layer is uniform except in case of the outer walls.

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